Special groups (n = 2)

In one group the father has been so severely attacked by his son that he had to be removed from the family. He died some minutes later due to a severe shock. We do not know why the father has been attacked. Subsequently the son interacted sexually with his mother. This pair produced altogether six litters. In the second case a sexually experienced male (father of 13 litters) got for social companion one of his adult daughters (mother of 7 litters). The female gave birth to male/female litter (see also French et al. 1984 for *S. oedipus*) which reproduced as well after removal of their parents (Table 1).

Discussion

The rather high frequency of inbreeding in incomplete groups cannot be interpreted as a mere accidental event. It is striking how often the groups violate the incest taboo, supposed such a phenomenon actually exists. The expulsion of the α-male in Gr. F (s. Table 2) (a similar situation was observed by Spichiger-Carlsson, 1982) may indicate that the incest taboo is only weakly realized in the common marmoset, and eventually influenced by the laboratory condition.

No less important seems to us the sexual interactions of a female with her father and the onset of pregnancy whilst the mother was sick and had to be treated medically (see also Epple 1967). This observation confirms the findings of Abbott (1984) and Evans and Hodges (1984) according to which the daughters may ovulate in the presence of their mother. Besides this the mere physical presence of their mother (= highest ranking female in the family) does not seem to be sufficient to prevent sexual behaviour of the α-male with his daughter(s). The result of this 'longterm study' contrasts to the observations in a 'shortterm study' of Anzenberger (1983), in which the presence of the mother and her offspring prevented sexual behaviour of the father and a strange female in a neighbouring cage, to which only the father and the strange female had access. However, we cannot exclude that the sickness of the α-female might have influenced the result, for example due to the eventuel loss of her α-status because of her physical inability. On the other hand Rothes (1974) hypothesis that marmosets are monogamous by status and not by emotional bond would be confirmed by that event.

Most striking to us has been the fact that in groups with unrelated members the reproductive reorganization was not incestuous but was based on the integration of the genetically unrelated group members, even when they were younger than the offspring of the remaining parent. We had, however, to prove, whether there has possibly existed a dominance-subordination relationship between the integrated and the family-born group members. In this case the avoidance of inbreeding could only be interpreted as a secondary phenomenon. But if incest avoidance must be regarded as a primary event, then the cognitive capacity of the common marmoset must be highly valued, especially since no group odor could be made responsible for that result (Epple, pers. comm.), except it would be genetically determined by a single Mendelian gene locus. To what extent young females experience an accelerated sexual maturation when becoming α-female cannot be answered at the moment (see also Tardif 1984).

We do not know whether infant transfer and/or infant-emigration/-immigration can be regarded as a regular event in the life of a marmoset group in order to offer a proper strategy for the reproductive reorganization of an uncomplete family. However, Dawson (1976) observed a rather frequent migration of juvenile *Saguinus oedipus geoffroyi* between neighbouring groups. At least in this tamarin species infant transfer seems to be a regular behaviour in the natural habitat.

Zusammenfassung

Reproduktive Reorganisation in unvollständigen Gruppen des Weißbüscheläffchens (Callithrix jacchus) unter Laborbedingungen

Die vorliegende Arbeit beschreibt Inzucht und deren Vermeidung in unvollständigen *Callithrix jacchus*-Gruppen. Untersucht wurden 20 Gruppen, die in drei Kategorien gegliedert wurden: 1. Gruppen, die ausschließlich verwandte Mitglieder enthalten; 2. Gruppen mit genetisch fremden Tieren a. entweder durch Integration infantiler/juveniler Tiere oder b. durch Integration eines adulten fremden Männchens in eine Weibchen-Gruppe (Mutter und vier Töchter). Insgesamt sechs Gruppen setzten die Reproduktion nach Verlust eines Elters fort. Die relativ große Anzahl von Familien (4 von 15 Gruppen), in denen nach Verlust des Elters Inzucht auftrat, kann nicht mehr als ein rein zufälliges Ereignis gewertet werden. Sehr auffällig ist die Einbeziehung der genetisch nicht verwandten Tiere in die reproduktive Reorganisation, in solchen Gruppen (n = 5), in die genetisch fremde Tiere integriert worden sind.

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Parent-offspring correlations for growth and reproduction in the vole *Clethrionomus glareolus* in relation to the Chitty Hypothesis

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Abstract

Studied in laboratory correlations between parents and offspring for weights and reproductive parameters in voles *Clethrionomys glareolus* from a non-cyclic population. Weight correlations were significantly positive in males and negative in females. Reproductive parameters correlated negatively. The latter correlations could be analysed further and be interpreted as due to a negative maternal effect. These findings contradict the Chitty Hypothesis of population regulation but may explain cyclic variations in weight and reproduction if external factors drive the cycles.

Introduction

Microtine cycles are characterized by small animals with high reproductive output during the increasing phase and large, slowly-reproducing animals at peaks. However, small adult animals with low reproduction occur during the declining phase (Krebs and Myers 1974; Taitt and Krebs 1985).

The Chitty Hypothesis (Chitty 1967, 1970, cf. also Krebs 1978), predicting regular genetic changes with cyclic fluctuations, has had a profound impact in explaining such morphological and reproductive variations. It states that timid, slowly-growing but high-reproducing animals are favoured in sparse and increasing pupulations whereas aggressive, large but slowly-reproducing animals are favoured in dense or peak populations. This mashinery should drive the cycles. Body growth and reproductive rates should thus be mainly genetically determined in microtine populations; body size and reproductive output should be closely correlated between parents and offspring. Animals caught in various population phases and brought to a laboratory should retain such correlations if there is low or random (density-independent) selection in the laboratory. These predictions were examined on the bank vole *Clethrionomys glareolus* which appears in both cyclic and non-cyclic populations in Sweden (Hansson and Henttonen 1985a).

Methods

The study was performed on animals which were bred for other reasons (Hansson and Henttonen 1985b; Hansson 1986) under laboratory conditions. The founding animals were taken from a clearly non-cyclic population in south Sweden (Hansson and Henttonen 1985a). Thus, it was possible to evaluate parent-offspring relations with regard to the pattern of population dynamics. The data were examined according to the rules of quantitative genetics but the relationships were mainly expressed as correlations (cf. Millar 1983) since certain prerequisites for heritability analysis may not have been present.

Bank voles were caught in live traps at Revinge (56° N) in 1980–83. The animals were kept as monogamous pairs after capture so the low mortality (19 and 8 % per year for wild-caught and

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laboratory-born animals respectively) was not density-dependent. The voles were caught in early autumn as young animals and kept on constant food (laboratory mouse pellets) and at a constant temperature (20 °C) for one year or until reproduction ended. Young of these animals, born in late summer-early autumn, were kept as monogamous pairs from an age of four months under the same laboratory conditions. Males were weighed every second week and the maximum weights recorded for each individual was used for the computations. In females, pregnancies caused exceptional weights so instead the weight one month before the first parturition was used. The length of pregnancy is ca 20 days in this species. Times of first parturition, litter sizes and number of litters as well as the total number of weaned young were recorded for all field-caught females (P) and their female offspring (F_1). Correlations were examined between weights and reproductive parameters of field-caught animals and the corresponding means of their laboratory-born offspring (Falconer 1981).

Results and discussion

Males showed a strong positive correlation in weights between parents and offspring (Table 1). Females showed a negative correlation, on the border of significance, for the same relationship. The number of litters, number of weaned young, mean litter size and start of reproduction were all consistently but non-significantly negatively related between female parents and offspring (Table 2).

Table 1. **Correlations between maximum body weight (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Sex	N	r	P
Males	12	0.81	< 0.01
Females	12	− 0.52	~ 0.05

There were thus clearly positive parent-offspring relationships in the body weights of the males. The mean weight ($\bar{x} \pm SD$) of parent (P) males was 24.3 ± 2.4 g and of offspring (F_1) males 23.8 ± 3.0 g so there was no significant change due to laboratory breeding. These relations have to be interpreted as genetic as no sources of error would cause a change in that direction for males (cf. below for females). The regression coefficients ($b \pm SE$) were 1.02 ± 0.24. According to Falconer (1981), this indicates a very high level of heritability. The generally negative relations in both body weights and reproductive parameters between female parents and offspring have to be interpreted as "a negative maternal effect" in analogy with Leamy (1981) and Millar (1983). Both these authors got consistent but low and often non-significant negative correlations in these parameters for both *Peromyscus leucopus* and *P. maniculatus*. They suggested that these negative correlations were due to well-fed females giving birth to large litters, where however each young had a low body weight. The female young were supposed to retain a comparatively low body weight as adults, to reproduce late and to produce small litters.

Table 2. **Correlations between reproductive parameters (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Reproductive parameter	N	r	p
Number of litters	13	− 0.25	NS
Weaned young	13	− 0.23	NS
Litter size	8	− 0.34	NS
Start of reproduction	8	− 0.40	NS

The applicability of this interpretation was examined as regards litter sizes and weight at weaning (Table 3). Litter sizes were significantly larger in the wild-caught (P) than in the laboratory-bred (F_1) females while female young at weaning (20 days) were heavier, although not significantly so, in the litters of F_1 females. However, a significantly lower